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THE OBSERVED EFFECTS OF MYXOMATOSIS ON RABBIT POPULATIONS AND BEHAVIOUR AND ON WILD LIFE GENERALLY

by R.M. Lockley
The Nature Conservancy, London

1. — *Introduction :*

i) *Physical effect on the individual rabbit.*

Myxomatosis of rabbits is a highly lethal disease caused by a virus of the pox group, visible only under the electronic microscope. The incubation period of the virulent strain B (Martin, 1936), established in Europe and Australia, varies betwen five and eight days. There follows an intense swelling and inflammation of the eyelids, spreading to the forehead and the base of the ears. A similar oedema containing virus occurs at the anal and generative orifices. At this stage the diseased rabbit usually becomes blind and insensitive to sound and although it grazes up to the last day (almost to the last hour and appears therefore not to be in great pain), it is unable to see or sense its way back to its burrow. Death occurs usually in the open between the tenth and fourteenth day. Strain B resembles the « fixed » virus of rabies in its constant virulence : its lethality is of the order of over 99 per cent.

ii) *Early research.*

Myxomatosis was first reported in 1898 from Brazil where Sanarelli found that European rabbits in his laboratory had no resistance to the disease. Subsequent tests on other animals including man have proved that the disease is specific to the European rabbit, *Oryctolagus cuniculus,* although rarely affecting the European hare, *Lepus* species. In 1943 Aragao showed that the disease is enzootic (and rarely fatal) in the Brazilian rabbit, *Sylvilagus.* He had earlier, in 1927, made the observation that myxomatosis might be effective in controlling the European rabbit in Australia. This possibility was investigated for the Australian Council for Scientific and Industrial Research by Sir Charles Martin who, as a result of experiments near Cambridge, England, was by 1936 able to report that the strain B of the myxoma virus was 100 per cent lethal in wild rabbits controlled in small outdoor enclosures under glass.

In 1936 Sir Charles asked my permission to make a large scale test by the introduction of the virus in rabbits on the island of Skokholm (well-isolated off the coast of Wales) which I was then farming. As I was very willing to abolish the uneconomic rabbit in order to obtain better grazing for my sheep, I agreed. Skokholm is approximately 240 acres large, and in that year was estimated to hold a climax population of 10.000 wild rabbits. In the autumn of 1936, 83 rabbits were caught, marked, inoculated with the same lethal B strain of the virus and released into burrows scattered all over the island. But during the ensuing winter the disease died out without any visible effect on the high rabbit population. The further attempts in the spring of 1937, and of 1938, failed in the same way : the disease killed the inoculated individuals but did not spread to uninoculated rabbits (Lockley, 1940).

At that time it was generally believed that insects were unimportant as vectors of the disease, and that direct contact was the chief cause of the spread of the virus. It is interesting to note that, with our present knowledge of the vectors of this virus and with public opinion as divided as it is today on this subject, scientists would hardly have embarked on experiments such as Sir Charles conducted — in the open at Cambridge, a low-lying area with mosquitoes present, for fear of the disease being spread by winged vectors. However it is also significent that the disease did not get out of control at Cambridge — for reasons which are indicated below.

Experiments were next carried out with the virus in Australia, from 1937 onwards, and it was proved that the stickfast flea, *Echidnophaga myrmecobii,* native to marsupials, attaches itself to rabbits and can act as a vector of the virus, although because of its sedentary habits, it is not so effective as the mosquito. It was not until 1950 however that, on reports of severe damage by rabbits to grazing, the Australian government consented to the experimental introduction of myxomatosis in the high rainfall and mosquito areas in the south-east (Bull, 1954).

iii) *Effects on rabbit populations in Europe.*

It was the spectacular and much published « success » of the disease in that area of Australia that encouraged the French doctor and biologist, Armand Delille, to introduce the virus (Martin's strain B) in 1952 in an attempt to destroy the plague of rabbits on his estate west of Paris. Part of my work for the Nature Conservancy included an early visit (1953) to Dr. Delille's estate, where I found that a typical « kill » of over 99 per cent associated with this virulent strain of the virus had taken place. At that time, Dr. Delille, like Sir Charles Martin, believed that the virus was not conveyed by insects, but only by contact. We now know that contact alone is not sufficient. The virus must enter the tissue by way of a bite or scratch.

Myxomatosis spread throughout France in a single year so that by the autumn of 1953 it had reached the French north coast departements, and had crossed to the nearest English counties of Sussex and Kent. (It is not part of this paper to discuss how it crossed to England, but it now appears that it may equally well have been carried naturally, by an insect vector blown by wind or temporarily attached to a migrating bird-gull, hawk or corvine predator — as deliberately by man).

The observed effects of the first outbreaks of myxomatosis on rabbit populations in south-eastern England were the same as in France and Australia : a near 100 per cent fatality. Early research on vectors in England by the Ministry of Agriculture (Muirhead Thompson) and the Nature Conservancy (R.M. Lockley) indicated the European rabbit's natural flea, *Spilopsyllus cuniculi,* as the main vector, and indeed the only vector capable of sustaining the high lethal attack on British rabbit populations which has followed. Certain mosquitoes, a tick and a mite and possibly some biting flies, convey the virus, but are not regarded as significant.

The failure of myxomatosis to control rabbits on Skokholm (as well as rabbits on certain other exposed islands since subjected to similar tests) is now explained by the proved absence or scarcity of this flea in these insular communities.

2. *The pattern of epidemics and transmission.*

The pattern of the outbreaks in the three countries principally affected up to 1954 has varied. In Australia the disease was deliberately introduced and encouraged by large scale inoculations all over that continent, but with varying success. In the warm areas of high rainfall where mosquitoes are numerous the first outbreaks resulted in nearly 100 per cent kill; but in dry cool areas myxomatosis has been slow to move and often unsuccessful, leaving warrens untouched. The European rabbit flea *Spilopsyllus* is unknown in Australia, where the marsupial flea *Echidnophaga* is by itself apparently an indifferent vector of the myxoma virus, although evidently effective in chain transmission with the mosquito. (In New Zealand, where there are no native mammals and no mammal fleas (Bull, 1953) myxomatosis has been introduced on a large scale but without more than a very local and impermanent effect (Filmer, 1953), in spite of the presence of biting flies and mosquitoes.)

In France, public opinion in the majority was hostile to the introduction of the disease; perhaps because of this the disease may have spread naturally rather than artificially, and its progress in France in general has followed river valleys and low-lying country where arthropod vectors are more numerous. It is known that the European rabbit flea *Spilopsyllus,* often in conjunction with mosquitoes, has been responsible as the main vector. The persistent attempts by the « chasseur » interest to re-establish the rabbit in France are likely to have the effect of establishing the disease (by providing continuous host-material for the virus) on an endemic scale.

In the cooler climate of the British Isles the admissible evidence points to considerable artificial introductions by farmers, foresters and other land-users. Since the rabbit-flea is the only important vector, and is known to be even more sedentary than its host the rabbit, it cannot move into fresh districts without its host; otherwise flea-borne outbreaks of the disease can only occur when the infected flea is transported either artificially by man, or by some natural agent such as a predatory animal, avian or mammal, which has been in contact with a rabbit, dying or dead of myxomatosis. It is safe to say that without the extensive introductions of the disease by man (generally by the transport of the dead or dying rabbit or of fleas collected from the same) myxomatosis might still be confined to a few outbreaks, instead of, as at the end of 1955, covering most of the counties of the British Isles.

3. *Rate of spread.*

The picture of myxomatosis outbreaks on the mainland of the British Isles which has emerged after three years'study is of a series of local epidemics which fan out from each centre. The same is observed in Australia and France. The rate at which the virus spreads depends on the density of local rabbit populations and their having adequate vector infestations. In a populous warren (of say 5 to 20 rabbits per acre) as each rabbit dies there is (in Britain) an increasing legacy of potentially infected fleas hungry (and partly mobile within or near the burrow or site of the carcase of the host) to bite and infect the remaining healthy rabbits. The lethality in these communities is then rapid, and often 100 per cent.

Yet the natural rate of spread in country of average rabbit population (say one rabbit to five acres) is quite slow and very difficult to measure (see Armour and Thompson, 1955). For example near my home in Pembrokeshire it was less than a mile in one month; but there are too many factors, including that of unreported artificial introductions, to make such a measuremnt scientifically significant.

In districts of the lowest rabbit densities myxomatosis, when it appears, although not less lethal, undoubtedly kills a lower percentage of the population because of its failure to reach individuals and small groups living in isolated warrens. It is these bypassed individuals and communities which are the source of potential reinfestations.

4. *Effects on surviving rabbits.*

The breeding cycle of the wild rabbit and that of its natural flea are intimately concurrent. The doe deposits her litter in a warm fur-lined nest underground the entrance to which she usually covers with earth. Here the female fleas, permanently attached to the doe, lay eggs which drop into the nest and rapidly hatch in the warmth. The larvae feed first on nest debris, then pupate. Further study is necessary to explain why the young rabbit, on leaving the nest at weaning (at three weeks of age), often carries few or no fleas. But this appears to be significant in view of the fact that, especially in populous warrens, the young rabbits leave, or are driven away by adults from, the main breeding warrens, and often wander and lie out in the open during the summer. They may thus escape infection during a local epidemic of myxomatosis in the main breeding centre.

On reaching maturity, that is of an age to breed, isolated rabbits travel and seek each other out and form the nucleus of a new colony in late winter and spring. These new colonists can re-establish in old warrens in which myxomatosis has, two months previously, wiped out the resident population. Sampling has shown that these rabbits are susceptible to, although they did not contract, myxomatosis, in spite of the presence of fleas surviving on or near carcases of rabbits which died of myxomatosis (personal observation).

Recovery from myxomatosis apparently has no adverse effect on the fecundity of the female rabbit. On the contrary we may expect that the rabbit will employ all its numerous biological resources, known and unknown, in the fight to recover its former strong population position. All the evidence of recent research indicates that the female rabbit produces more live young per litter under the conditions of abundant food supply — which would apply in those areas denuded by myxomatosis, which formerly supported large populations. This resilient fecundity is likely to be a formidable obstacle to the success of any government-supported campaign (as in Australia and Great Britain) to exterminate the wild rabbit. However, it is obvious that, failing extermination, rabbits are going to be scarce for some years in those countries affected by myxomatosis.

5. *Effects on other animals.*

It is still too early to state with any precision the after-effects of the destruction of large rabbit populations upon other animals, and especially upon those species which were known to prey extensively upon rabbits. But, in general, there have been remarkably few clearly defined effects upon these predators; and it would seem as if there has been a rapid adjustment to the altered food supply. The current investigation into the status of the buzzards *(Buteo buteo)* in Britain by N.W. Moore has shown a considerable reduction in the number of live young reared by this bird in the critical year (1955) of low rabbit numbers. This low breeding success will automatically reduce the number of buzzards, even if no deaths of adult birds occur through malnutrition.

Foxes have shown greater interest in poultry and possibly lambs, and fawns of roe-deer, but not on any formidable scale : they have, however been successfully controlled by farmers and hunting establishments in anticipation of this danger.

Stoats are said, again without adequate scientific proof, to have become scarcer in Britain, and this has been put down to lack of food leading to poor breeding success as in the case of the buzzard. Stoats are also said to be taking freely grey squirrels, which are undoubtedly much scarcer in Britain. However, it is to be noted that large numbers of grey squirrels have been killed recently by man for the sake of a bounty paid by the government, and this together with other possible unexplored factors may have also contribute to their scarcity.

Rats are reported to be much scarcer in Britain generally. Again it is not easy to measure any change in rat population with accuracy, but reports by regional pest control officers indicate the strong probality that foxes, buzzards and other predators are feeding more freely on rats in the absence of rabbits. It is also suggested that as rabbit-burrows gradually fall in and silt up there will be less underground cover to harbour rats.

In France, it is commonly reported that hares have become more numerous and have spread into new districts as a result of the scarcity of its food competitor the rabbit, and of the removal of rabbit fences which restricted wandering.

Without doubt the immediate quantitative and qualitative improvement in open and woodland pastures and heaths due to the lack of grazing by rabbits has benefitted those wild species — hare and deer especially — which compete for this food supply. The long-term changes in the vegetation of such sites which the removal of over-grazing and soil-erosion by rabbits is bringing about, resulting in more successful regeneration of palatable grasses, plants and trees, and the reduction of weeds and unpalatable species, will further affect beneficially the economy of the larger grazing mammals, both wild and domestic. This must be especially true of countries, such as Australia and the British Isles, where the rabbit is an introduced species, and known thereby to have disturbed the indigenous ecology with disadvantage from the economic standpoint.

6. *Summary and conclusion.*

The immediate observed effects of the lethal strain of myxomatosis on rabbit populations are described. They are initially calamitous for the species. An accurate assessment or forecast of the future of rabbit populations is difficult, at least within the brief period during which this disease has attacked the European rabbit in the field. But it is clear that extermination, once considered a probability, is now hardly a possibility. The species is showing signs of recovery.

A fresh aid to recovery is the appearance of localized attenuated strains of the virus in Australia, France and England, resulting in as low as 50 per cent lethality, and leaving half the number of rabbits in each affected warren immune. Unless governments take strong action to exterminate these survivors it is easy to foresee that rabbits will gradually return to their former strength, with the virus gradually weakening and myxomatosis becoming an enzootic non-fatal disease as in the American *Sylvilagus,* from which source the virus first attacked the European *Oryctolagus.*

REFERENCES

ARAGAO, H. de B. (1943), *Mem. Inst. Ozwaldo Cruz.* 38 : 93.
ARMOUR, C.J. & THOMPSON, H.V. (1955), *Annals Appl. Biol.* 43 : 511.
BULL, L.B. (1954), B.B.C. broadcast, September 11th.
BULL, P.C. (1953), *N.Z. Journ. Sci. Tech.* B. 34 : 367.
FILMER, J.F. (1953), *N.Z. Journ. Agri.* 87 : 402.
LOCKLEY, R.M. (1940), *Nature, Lond.* 145 : 767.
MARTIN, C.J. (1936), *Coun. Sci. Ind. Res. Bulletin* 96.

Summary

The immediate observed effects of the lethal strain of myxomatosis on rabbit populations and behaviour are initially calamitous, resulting in over 99 per cent mortality. The indirect effects of the scarcity of rabbits on other animals have been difficult to measure accurately in the short period during which the disease has been epidemic in Australia and Europe. Predators of the rabbit seem to have adjusted quickly to the changed food supply, by taking other prey or by breeding less successfully, or both.

The immediate quantitative and qualitative improvement in grazing vegetation due to the removal of overgrazing and soil-erosion by rabbits has benefitted some species, especially deer and hare. The long-term improvement resulting in more successful regeneration of palatable grasses, plants and trees will affect beneficially the economy of larger grazing animals, both wild and domestic, and this improvement is already evident. It may last for several years, depending on the density of rabbit populations.

However there are signs that the rabbit is recovering its numbers slowly, while weak strains of the virus have appeared which already are aiding this recovery and unless governments take drastic action to exterminate the

survivors, myxomatosis may shortly become a non-fatal enzootic disease of the European rabbit, as it is of the Brazilian species.

RESUME

Les effets immédiats de la forme mortelle de myxomatose sur les populations et le comportement des lapins sont tout d'abord calamiteux et entraînent 99 % de mortalité. Il a été difficile d'évaluer exactement les effets indirects produits par la diminution des lapins sur d'autres animaux au cours de la brève période pendant laquelle l'épidémie a sévi en Australie et en Europe. Les prédateurs du lapin semblent s'être adaptés rapidement au changement de régime, soit en s'accoutumant à d'autres proies, soit en réduisant leur fécondité, parfois de l'une et de l'autre manières.

L'amélioration immédiate, quantitative et qualitative, de la végétation herbacée, résultant de la suppression du lapin, cause de surpâturage et d'érosion, a été bénéfique pour certaines espèces, cerfs et lièvres notamment. A longue échéance sera favorisée la régénération des herbes secondaires, plantes herbacées et arbres; celle-ci ne peut manquer d'être favorable aux ruminants de plus grande taille, sauvages ou domestiques, et se fait déjà sentir. Cette situation est susceptible de durer pendant plusieurs années, et dépendra de la densité des populations de lapins.

Cependant, certains signes annoncent que les lapins récupèrent lentement et que des souches atténuées du virus se seraient manifestées et favoriseraient ce rétablissement. A moins que les gouvernements ne prennent des mesures en vue de l'extermination des survivants, la myxomatose pourrait bien évoluer jusqu'à devenir une maladie endémique du lapin européen, à l'instar de ce qui se passe dans le cas de l'espèce brésilienne.